

FRUTEXITES FROM STROMATOLITES OF THE GUNFLINT IRON FORMATION OF CANADA, AND ITS BIOLOGICAL AFFINITIES*

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ABSTRACT

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The microfossil *Frutexites* is known from many Palaeozoic and some Proterozoic carbonate sedimentary rocks. We recently found unusually well-preserved examples in the early Proterozoic Gunflint Iron Formation of Ontario, Canada. These are preserved in chert, along with other microfossils of the Gunflint microbiota. The Gunflint examples have previously been described as laminated, columnar-branching microstromatolites. We have found narrow tubes (interpreted as trichome moulds) axially placed in many of the microcolumns. By comparison with extant organisms, we interpret *Frutexites* as a thick-sheathed scytonematacean cyanophyte. These are the oldest known fossil scytonemataceans. They apparently grew within mats of other microorganisms. These probably were photosynthetic organisms, which may have significant implications in the interpretation of some occurrences, such as in the fore-reef facies of Devonian reefs in Western Australia.

INTRODUCTION

The Gunflint microbiota from southern Ontario is famous as the first well-preserved assemblage of Precambrian microfossils to be described (see Awramik and Barghoorn, 1977, for references to earlier work). Its isotopic age is not well established, but is older than 1685 ± 24 Ma, and may be approximately 2000 Ma old (for a discussion see Knoll et al., 1978). The microfossils are organically preserved in dark grey to black cherts, and infrequently as iron-oxide replacements or casts in red cherts. The dominant taxa are found in both modes of preservation in the Gunflint Iron Formation

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and many of those organically preserved in the Gunflint are found as hematite replacements and casts in the Frere Formation of Western Australia (Walter et al., 1976). The fossils described here as *Frutexites microstroma* sp. nov. are preserved as organic matter permineralised by silica in black stromatolitic chert. We have been fortunate in finding them preserved this way as this has allowed the observation of structures normally obscured by iron oxides in the much commoner preservational mode. It is this that has allowed a new interpretation of *Frutexites* Maslov.

All known occurrences of *Frutexites* or closely comparable structures are within stromatolites which, except for the Gunflint example, are composed of carbonates. Maslov (1960) erected the new genus and species *Frutexites arboriformis* for examples from the Ordovician of the Siberian Platform. The generic name has also been applied to microfossils in stromatolites of the fore-reef facies in Devonian reefs of Western Australia (Playford et al., 1976) and closely comparable fossils have been described from the middle Proterozoic Belt Supergroup of the western U.S.A. (Horodyski, 1975), Upper Riphean of the U.S.S.R. (Raaben and Zabrodin, 1972, Plate 10), Cambrian of France (Doré, 1962), and Jurassic of Poland (Szulczewski, 1963, 1968; Niegodzisz, 1965; Gizejewska and Wieczorek, 1977). The Gunflint examples have been described previously by Moorhouse and Beales (1962) and Hofmann (1969). Other microstromatolitic structures are also known (e.g., Larsson, 1973, p. 66; Haslett, 1976, p. 576; Edhorn and Anderson, 1977, p. 120) but do not appear to be more than superficially comparable to *Frutexites*. Abiogenic (?) dendrites also superficially resemble *Frutexites*.

SYSTEMATIC PALAEONTOLOGY

Kingdom Procaryota
 Division Cyanophyta
 Class Hormogoneae
 Order Nostocales
 Family Scytonemataceae
 Genus *Frutexites* Maslov 1960

Type species

Frutexites arboriformis Maslov 1960, from Ordovician stromatolites of the Siberian Platform.

Diagnosis

An alga (?) forming calcareous cushions or turf of vertically or radially arranged filaments with false branches and with sheaths which are narrow at the bottom and widen considerably towards the periphery (translated from Maslov, 1960, p. 60).

Description of the type species

The algae form nodular cushions firmly attached to the substrate which are perforated by radially diverging and branched sheaths. The latter are thin at the base and rapidly become wider above or towards the margin of the nodular cushion. In the specimens studied the cavities due to the sheaths are filled with iron hydroxide and thus are clearly distinguishable against the bright background of carbonate. The sheaths have a width of 25–30 μm . In the clusters of sheaths, the empty ones are filled with ferruginous material forming “funnels” and collars which reach a width of 50 μm and more. Occasionally, circular spaces, each of which is filled with one crystal of carbonate, are found inside the ferruginous material. Their width is from 15 to 20 μm , occasionally 30 μm and their height 20–25 μm . It is possible that these are the remains of cells or heterocysts of the algae described. In the “shrub” with the slight accumulation of iron, chains of circular or polygonal cells 10–20 μm in diameter are found surrounded by thick iron coatings (translated from Maslov, 1960, p. 60–61).

Frutexites microstroma Walter and Awramik sp. nov.

“Branching pillar-like pattern”, Moorhouse and Beales 1962 (fig. 1b; p. 101)

“Microstromatolites”, Hofmann 1969 (plate 8; p. 15)

Material. Abundant examples in stromatolites from the Gunflint Iron Formation at Winston Point, 9 km west of Schreiber, Ontario, north shore of Lake Superior, Canada (locality 78418b of Hofmann, 1969). The type specimen is that illustrated in Fig. 6, in thin section YPM23026 deposited in the Peabody Museum, Yale University.

Name. In reference to Hofmann’s (1969) designation.

Diagnosis. *Frutexites* frequently with axially placed single tubes 1.0–2.7 μm wide.

Description. It is apparent from Hofmann’s (1969) descriptions and our work that *F. microstroma* occurs in his stromatolite forms A, D, E and F. Our material comes from a single large specimen which contains an intergrading series of stratiform and columnar-branching stromatolites; the microfossil distribution within these stromatolites has been described by Awramik (1976). *F. microstroma* is locally abundant but sporadic at the bases of stromatolite columns (cf. *Kussiella*) and in the underlying stratiform stromatolites. Hofmann (1969) reports “microstromatolites” from stromatolites very similar to cf. *Kussiella* (his forms A and D) from the same locality as our specimen (Winston Point) and also from other localities (they also occur in his stromatolite Form E). Hofmann’s (1969) Form F from his locality 78418b is from part of the specimen we have used here.

The microcolumns of *F. microstroma* are oriented perpendicular to the stromatolite laminae almost invariably (Plate I (1)); one example of slightly inclined microcolumns was noted. As is well illustrated by Hofmann (1969, plate 8), the perpendicularity results in a fan-like arrangement of the microcolumns over the convexities of the stromatolite laminae. The microcolumns

are rare on the steeply sloping laminae on the flanks of cf. *Kussiella* columns, but where they occur, they are still perpendicular to the laminae.

F. microstroma ranges in form from undulose stratiform layers 2.0–30.0 μm thick (Plate I (2)) to laminae with small protruding pustules about 5 μm wide and 50 μm high, to erect branching microcolumns (Plate I (3–6) and Plate II (1)). The microcolumns are 5–120 μm wide and up to 450 μm high. The branching style is from slightly to markedly divergent. Those microcolumns that branch, invariably do so upwards. The microcolumns vary from cylindrical to turbinate to wispy and irregular.

The microcolumns consist of upwardly convex laminae which range from prolate through steeply convex to gently convex. The laminae usually bend down to coat the column margins. The laminae are 0.7–2.7 μm thick, with parallel, abrupt borders, and have a banded appearance (Plate I (5,6)).

The irregular wispy microcolumns and the smaller of the regular microcolumns frequently have a single tube interpreted as a trichome mould along the column axis (Plate I (4), (7)). Single, axial, trichome moulds occur infrequently in the larger columns (Plate I (3, 6, 8)). The only other microfossils found within the microcolumns are rare *Huroniospora*-like spheres.

The tubes are 1.0–2.7 μm wide, with a modal width of 1.5–2.0 μm . No septae, constrictions, tapering, or enlarged regions in the tubes were observed. The tubes lie prostrate and weakly intertwined within the undulose stratiform parts of *F. microstroma*, where they are slightly sinuous. In the

PLATE I

Fig. 1. Erect, branching, *Frutexites microstroma* microcolumns in cf. *Kussiella* columnar stromatolite from Winston Point. Gunflint. Thin section 7017 h-3; stage coordinates 124.5 $\times$ 17.0. Bar equals 1 mm.

Fig. 2. Wavy micro-laminated to pustular development of *F. microstroma* along lamina of *Stratifera* from Winston Point. Gunflint. Thin section 7016 h-1; stage coordinates 95.2 $\times$ 6.4. Bar equals 0.5 mm.

Fig. 3. Group of cylindrical and turbinate *F. microstroma*, oriented normal to laminae in *Stratifera* from Winston Point. Gunflint. Thin section 7016 j-2; stage coordinates 95.9 $\times$ 16.4. Bar equals 100 μm .

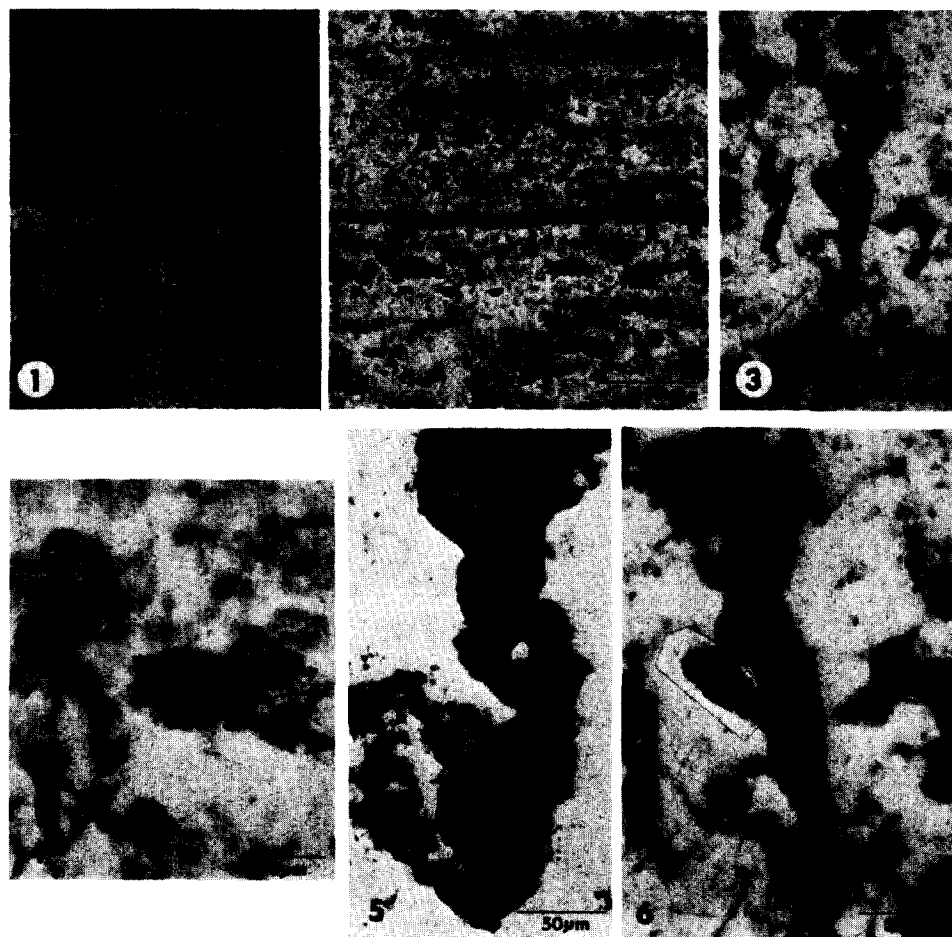
Fig. 4. Turbinate to wispy and irregular *F. microstroma* in *Stratifera*; laminae oriented left to right, prostrate trichome mould indicated by arrow. Probable example of trichome branching immediately to left of arrow. Gunflint. Thin section 7016 j-1, stage coordinates 96.8 $\times$ 9.1. Bar equals 50 μm .

Fig. 5. Microlaminated, erect branching *F. microstroma* in cf. *Kussiella* from Winston Point. Gunflint. Thin section 7017 h-3; stage coordinates 127.7 $\times$ 22.2. Bar equals 50 μm .

Fig. 6. Type specimen of *Frutexites microstroma* in *Stratifera* from Winston Point. Gunflint. Arrow points to trichome mould at base of column. Thin section 7016 j-2; stage coordinates 95.4 $\times$ 16.4; YPM 23026. Bar equals 50 μm .

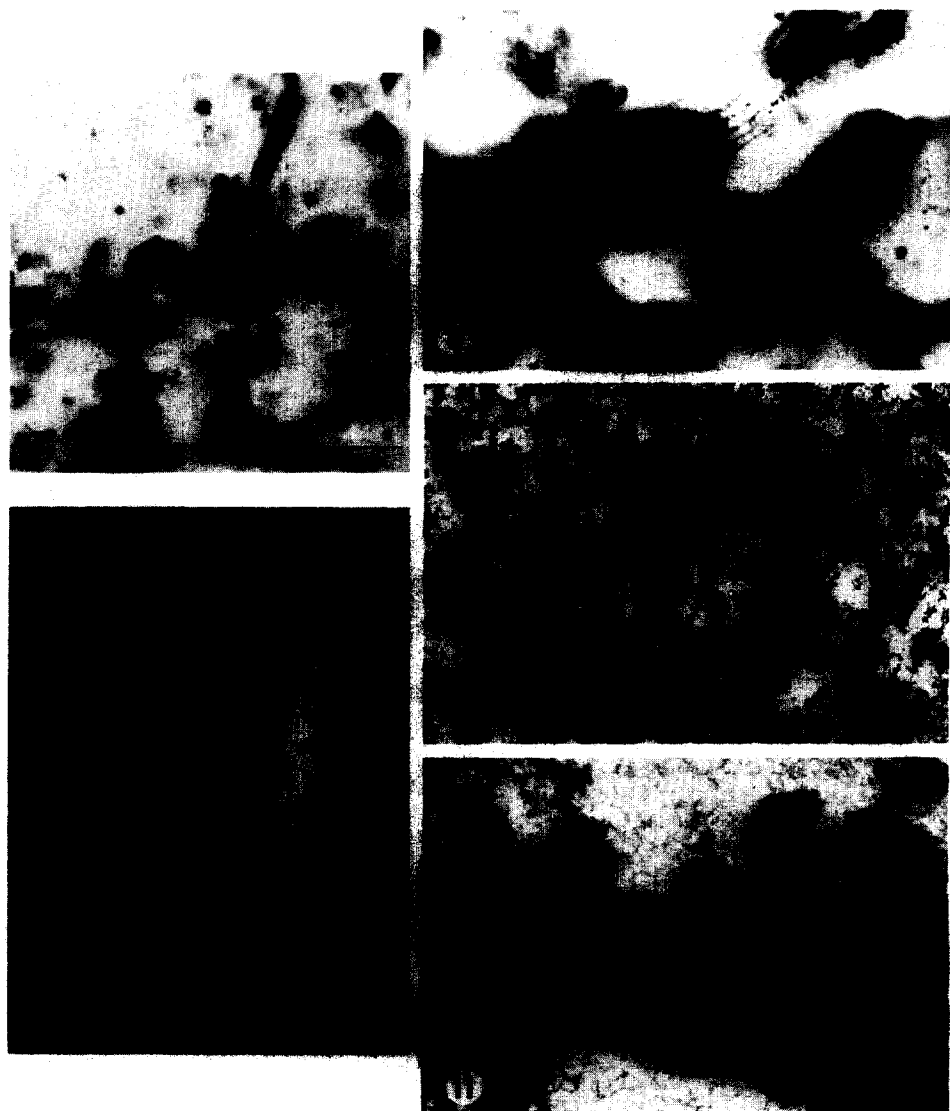
microcolumns the tubes are straight or gently curved. We have observed several examples of apparent branching of tubes (e.g., Plate I (4)). The observed angles of branching are $80-90^\circ$ at the points of branching, decreasing to $30-50^\circ$ as the branches elongate. Tubes up to $60\text{ }\mu\text{m}$ long were observed. Frequently they terminate upwards at the bases of convex laminae capping columns. Less frequently they penetrate column tops.

Comparisons. *F. microstroma* is distinguished from *F. arboriformis* Maslov by the presence, at least sporadically, of axial tubes (mould of trichomes).



GROWTH OF *FRUTEXITES MICROSTROMA*

Laminae within the Gunflint stromatolites examined in this study are 30–45 μm thick, both where *F. microstroma* is abundant and where it is absent. Where it is abundant, other microfossils are generally absent from the stromatolite laminae; elsewhere in these same stromatolites, it is apparent that the laminae were constructed by *Gunflintia minuta* Barghoorn and *Huroniospora* Barghoorn (Awramik, 1976; Awramik and Semikhatov, sub-



mitted). No microstructural features can be correlated with the presence of *F. microstroma*, and so we consider that this organism grew within laminae previously constructed by *Gunflintia* and *Huroniospora* (Monty, 1976, p. 219, has described a similar occurrence within Holocene cyanophytic mats, although in that example there is some consequent lamina thickening).

The growth sequence of *F. microstroma* can be interpreted as follows. Growth originated within the upper portions of previously established laminae with the first appearance of dark microlaminated masses or pustules. These then grew laterally, producing a felt of trichomes oriented subparallel to the laminae (Plate I (4)). Growth perpendicular to the laminae then resulted either from the upward growth of some trichomes, or from trichome branching (Plate I (4,7)). Upward growth continued, extracellular sheath material was produced periodically, giving rise to lamellated sheaths, and the bushy columns characteristic of *Frutexites microstroma* developed. This growth could all but obliterate original stromatolite laminations.

The lack of other microfossils and organic matter in *Frutexites*-rich areas could be due to the oxidation of the other microfossils and organic material by O₂ produced by *F. microstroma* (assuming it was a cyanophyte and performed oxygenic photosynthesis), or to the activities of aerobic heterotrophic bacteria living within the *F. microstroma* communities.

BIOLOGICAL INTERPRETATIONS

Maslov (1960) interpreted *Frutexites* as iron hydroxide-filled cavities pseudomorphic after cyanophyte sheaths. This interpretation was supported by Szulczewski (1968), although he earlier (Szulczewski, 1963) considered them as ferruginous deposits formed directly by cyanophytes. Niegodzisz (1965) considered the iron hydroxides to be a replacement of carbonate ori-

PLATE I (cont'd)

Fig. 7. Turbinate to cylindrical *F. microstroma* with erect tube or trichome mould. In *Stratifera* from Winston Point. Gunflint. Thin section 7016 h-1; stage coordinates 103.1 × 11.0. Bar equals 50 μm.

Fig. 8. Trichome moulds of prostrate to inclined *F. microstroma* in cf. *Kussiella* from Winston Point. Gunflint. Laminae are convex up towards the top of the plate. Thin section 7017 h-3; stage coordinates 123.9 × 19.9. Bar equals 10 μm.

Fig. 9. Microstructure composed of hematitic *Frutexites* in Upper Riphean (Minyar Suite) columnar stromatolites from the southern Urals. From thin section illustrated by Raaben, plate 10, in Raaben and Zabrodin, 1972. Bar equals 50 mm.

Fig. 10. Enlargement of Fig. 9 illustrating the erect, branching hematitic *Frutexites* columns. Bar equals 0.5 mm.

Fig. 11. Hematitic *Frutexites* from lower Missoula Group, Glacier National Park, Montana. From thin section illustrated by Horodyski, 1975, fig. 10. Thin section RHG 229c, stage coordinates 123.7 × 30.0. Bar equals 100 μm.

ginally encrusting the cyanophyte filaments. Both Hofmann (1969) and Horodyski (1975) suggested a bacterial origin for the "microstromatolites" they described, because of the narrowness of the microcolumns and the thinness of the lamination (i.e., the microlaminations were considered too small to be produced by cyanophytes).

F. microstroma frequently has recognisable axial tubes (trichome moulds) within the erect, branching microcolumns and prostrate tubes in the horizontal growth habit. Though few convincing examples of branching of the tubes have been observed, it seems that branching of prostrate trichomes produced erect trichomes and their enclosing microcolumns. Here, both described species of *Frutexitis* are interpreted as cyanophytes in which usually only the mucus sheaths (the microcolumns) are preserved. We refer them to the Scytonemataceae. Comparisons can be made with the extant scytonematacean genera *Tolypothrix* (specifically *T. lithophila*, Bourrelly, 1970, pp. 388, 389, 392), *Scytonema* (Geitler, 1932, pp. 740–787) and *Petalonema* (Geitler, 1932, pp. 788–797). The irregularity and massiveness of the *Frutexitis* sheaths can be compared with similar features in the sheaths of *Petalonema alatum* Berkeley (Geitler, 1932, pp. 789–792); this species has sheaths 57–115 μm wide. The lamina profile within *F. microstroma* microcolumns is very similar to that in the sheaths of *Tolypothrix lithophila* (Bourrelly, 1970, p. 389). The acute angle of branching of the erect *Frutexitis* microcolumns is also similar to that of *T. lithophila*. Lack of cellular preservation prevents detailed comparison with the branching of scytonematacean (and stigonematacean) cyanophytes; the angle of branching does, however, approach 90° at the site of branching, a characteristic of both of these families. The prostrate and erect habit of *F. microstroma* resembles the habit of various species of *Scytonema* (Geitler, 1932, pp. 740–787; Bourrelly, 1970, pp. 396–398), in particular *S. myochrous* (Dillw.) Ag. (see Bourrelly, 1970, pp. 396–397).

A rivulariacean affinity is considered unlikely because rivulariaceans usually (a) are smaller, (b) lack a well-developed prostrate growth habit, and (c) have a growth habit in which the ends of branches are open, exposing the trichome, or at least where the sheaths and trichomes are markedly tapered. Rivulariaceans also tend to form hemispherical tussocks of radially oriented filaments in both Holocene (Monty, 1976) and ancient stromatolites (Bertrand-Sarfati, 1972).

The possibility of a stigonematacean affinity cannot be excluded, although *F. microstroma* is quite unlike the more complex forms of that family. The scytonemataceans are heterocystous (they have within the trichomes specialised cells — heterocysts and akinetes). Lack of cellular preservation prevents us from knowing whether *F. microstroma* was also heterocystous, although the trichome moulds, where they are well preserved, are uniform in width.

In referring *Frutexitis* to the Scytonemataceae, we stress that not one extant member of this family exhibits all the characteristics found in the

Gunflint *Frutexites* but, as a group, the Scytonemataceae offer the most satisfactory and consistent comparison.

PRECAMBRIAN RECORD OF *FRUTEXITES* AND THE SCYTONEMATACEANS

In recent algal mats, scytonemataceans produce a laminated-radial fabric which is the result of the vertical growth of erect filaments alternating with prostrate filaments oriented along, and in some cases forming, horizontal or convex laminae (Monty, 1976, p. 118). Ancient stromatolitic microstructures exhibiting this fabric have been attributed to scytonematacean activity. Gebelein (1974) recognised such a fabric in the approximately 2000 Ma old Rocknest Formation in northern Canada (Hoffman, 1976). Late Riphean to Vendian (late Proterozoic) stromatolites of the northwestern Sahara also have a possibly scytonematacean fabric (Bertrand-Sarfati, 1972). Raaben (in Raaben and Zabrodin, 1972, plate 10) illustrated an unnamed stromatolite from the Late Riphean Minyar Formation of the U.S.S.R. with a microstructure similar to *Frutexites*. Our study of Raaben's material indicates that this microstructure is composed entirely of *Frutexites* cf. *arboriformis* Maslov, with hematitic replacement of the original filaments (Plate I (9, 10)). Horodyski (1975) reported *Frutexites*-like "microstromatolites" from within carbonate stromatolites of the approximately 1100 Ma old Missoula Formation of Montana. After examining Horodyski's material we consider that the microstromatolites can be identified as *F.* cf. *arboriformis* (Plate I (11)).

To the best of our knowledge no organically-preserved scytonemataceans have been reported previously. The following families of cyanophytes are now considered to have representatives in early Proterozoic rocks: Chroococcaceae, represented by *Corymbococcus hogkissii* Awramik and Barghoorn and some forms of *Huroniospora* Barghoorn from the Gunflint Iron Formation, and several species in the Kasegalik Formation, Belcher Islands (Hofmann, 1976); Entophysalidaceae, represented by *Eoentophysalis* Hofmann from the Kasegalik Formation; Oscillatoriaceae, represented by *Halythrix* Schopf from the Kasegalik Formation, and probably some filamentous forms from the Gunflint Iron Formation; Nostocaceae, possibly represented by *Gunflintia minuta* Barghoorn from the Gunflint Iron Formation (Licari and Cloud, 1968; Awramik and Barghoorn, 1977), and *Petra-phaera vivescenticula* Nagy from the Transvaal Dolomite (Nagy, 1974, 1978); and now Scytonemataceae, represented by *F. microstroma*. There are also possible representatives of the Rivulariaceae (Nagy, 1978) and Pleurocapsaceae (Hofmann, 1976).

All known *Frutexites* except those found in the Gunflint are preserved as iron oxide (hematite) replacements or coatings on hollow tubes filled with sparry calcite. Horodyski (1975, p. 231) suggested that the hematite represents oxidised iron sulfide precipitated initially during a bacterial decomposition of organic matter. Playford et al. (1976, p. 558) considered the

possibility that algae precipitated iron but favored iron bacteria living in association with the algae as the agents for the concentration of iron oxides. The well-developed lamellar structures interpreted as the sheaths in *Frutexites* lead us to consider a modified algal origin for the iron oxides. Iron chelation within sheaths of cyanophytes is known (Walsby, 1974), and indeed *Scytonema* is characterised by lamellar sheaths heavily pigmented by scytonemine (see Fritsch, 1945, p. 796). Ion microprobe analyses of the scytonemine-pigmented sheaths of *Lyngbya* (R. Conrad, analyst) confirm the presence of iron. The mechanism of transformation of chelated iron to hematite is unclear, but is probably dependent on the availability of oxygen. The Gunflint *Frutexites* are preserved as organic matter without hematite.

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